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Received: 11 December 2020 | Revised: 7 October 2021 | Accepted: 18 October 2021

DOI: 10.1002/eap.2589

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Tree growth response to drought partially explains regional-scale growth and mortality patterns in Iberian forests

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Abstract

Tree-ring data has been widely used to inform about tree growth responses to drought at the individual scale, but less is known about how tree growth

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Funding information
Fundación BBVA, Grant/Award Number: 2018 Leonardo Grant; Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Grant/Award Number: RTA2006-00117; Ministerio de Ciencia e Innovación, Grant/Award Numbers: RTI2018-096884-B-C31, RTI2018-096884-B-C3, AGL2017; Xunta de Galicia, Grant/Award Numbers: PGIDIT06PXIB502262PR, GRC GI-1809; Unitatea Executiva pentru Finantarea Invatamantului Superior, a Cercetarii, Dezvoltarii si Inovarii, Grant/Award Number: PN-III-P1-1.1-TE-2019-1099

Handling Editor: Juan C. Corley

sensitivity to drought scales up driving changes in forest dynamics. Here, we related tree-ring growth chronologies and stand-level forest changes in basal area from two independent data sets to test if tree-ring responses to drought match stand forest dynamics (stand basal area growth, ingrowth, and mortality). We assessed if tree growth and changes in forest basal area covary as a function of spatial scale and tree taxa (gymnosperm or angiosperm). To this end, we compared a tree-ring network with stand data from the Spanish National Forest Inventory. We focused on the cumulative impact of drought on tree growth and demography in the period 1981–2005. Drought years were identified by the Standardized Precipitation Evapotranspiration Index, and their impacts on tree growth by quantifying tree-ring width reductions. We hypothesized that forests with greater drought impacts on tree growth will also show reduced stand basal area growth and ingrowth and enhanced mortality. This is expected to occur in forests dominated by gymnosperms on drought-prone regions. Cumulative growth reductions during dry years were higher in forests dominated by gymnosperms and presented a greater magnitude and spatial autocorrelation than for angiosperms. Cumulative drought-induced tree growth reductions and changes in forest basal area were related, but initial stand density and basal area were the main factors driving changes in basal area. In drought-prone gymnosperm forests, we observed that sites with greater growth reductions had lower stand basal area growth and greater mortality. Consequently, stand basal area, forest growth, and ingrowth in regions with large drought impacts was significantly lower than in regions less impacted by drought. Tree growth sensitivity to drought can be used as a predictor of gymnosperm demographic rates in terms of stand basal area growth and ingrowth at regional scales, but further studies may try to disentangle how initial stand density modulates such relationships. Drought-induced growth reductions and their cumulative impacts have strong potential to be used as early-warning indicators of regional forest vulnerability.

KEYWORDS
basal area increment, drought vulnerability, mortality, national forest inventory, Spain, stand structure, tree growth

INTRODUCTION

The recent increase in land surface temperatures and the occurrence of climate change-related extreme events, such as heat waves and droughts, have triggered forest growth reductions and mortality events in many temperate and Mediterranean regions (Allen et al., 2010, 2015). Notably, recent hotter droughts are characterized by increased air temperatures, which raise the atmospheric demand for water, exacerbating water storage problems, and disrupting the functioning of trees by reducing their growth rates and limiting forest carbon uptake (Anderegg et al., 2015; Babst et al., 2019). Extreme droughts or their accumulated effect over time (Peltier et al., 2016) stress trees and deteriorate their vigor, ultimately triggering their mortality (Cailleret et al., 2017, 2019; DeSoto et al., 2020; Jump et al., 2017). Nevertheless, how all these processes scale up from trees to forest dynamics and their influence on carbon and water fluxes at the ecosystem level, remains unresolved (Anderegg et al., 2016; Babst et al., 2018).

Radial growth is a reliable proxy of tree vigor and so it can be used to study the effects of climate change on trees (Marchand et al., 2019). Drought events can lead to abrupt growth reductions that can last for several years (Schweingruber, 1986). However, how tree growth reacts

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to drought may depend on multiple factors (Anderegg et al., 2013), with longer and more severe droughts most likely resulting in greater growth reductions (Gao et al., 2018). In the worst case, intense droughts can induce irreversible growth reductions preceding tree death (Cailleret et al., 2017; Camarero et al., 2015; DeSoto et al., 2020; Sánchez-Salguero et al., 2012). Even when trees survive drought, there might be lagged effects of water deficit (i.e., "drought legacy effects"), that tend to be stronger in regions where tree performance is strongly constrained by drought (Anderegg et al., 2015) as is the case of the Mediterranean region (IPCC, 2018). However, a recent study found that Mediterranean Spanish forests are resilient to recent droughts in terms of canopy greenness derived from satellite imagery (Khoury & Coomes, 2020), pointing out that different sources of information need to be combined in order to get more complete, long-term pictures of how forests respond to drought.

Tree growth sensitivity to drought also varies across tree populations, tree species, functional groups (i.e., gymnosperms, angiosperms), and forest biomes (Anderegg et al., 2015; D'Orangeville et al., 2018; Gazol, Camarero, et al., 2017; Gazol, Ribas, et al., 2017; Peltier et al., 2016; Serra-Maluquer et al., 2019; Vilà-Cabrera & Jump, 2019). Lagged effects on tree growth seem to be higher and last longer in gymnosperms than in angiosperms (Anderegg et al., 2015), probably because angiosperms have a more efficient hydraulic and leaf transpiration systems compared to gymnosperms (Brodribb & McAdam, 2013). Furthermore, angiosperms and gymnosperms have different xylem traits in terms of wood anatomy and density, which results in different strategies to avoid drought-induced cavitation (Brodribb et al., 2010; Carnicer et al., 2013; Rosas et al., 2019). For instance, Gazol et al. (2018) found that gymnosperms from drought-prone Spanish regions presented more conspicuous drought-induced growth reductions and lower growth resistance; sensu Lloret et al., 2011 than angiosperms from wet, temperate areas. The sensitivity of tree growth to drought has important implications to understand the resilience capacity of forests (Lloret et al., 2011). However, reconstructions of forest growth using tree-ring records are affected by sampling biases related to the selection of representative and dominant individuals (Alexander et al., 2018; Brienen et al., 2017), and it remains unclear how tree-ring based responses to drought scale up to understand forest dynamics processes such as forest growth, ingrowth, and mortality (Kannenberg et al., 2019).

Shifting dynamics in forest growth, productivity, and mortality relies on the interaction between climate conditions, structure, and composition (Ruiz-Benito, Ratcliffe, Jump, et al., 2017; Vayreda et al., 2016). Most large-scale studies on forest dynamics take advantage of forest inventory data that provide tree-level information, gathered systematically and periodically at large spatial extents (Kunstler et al., 2016; Liang et al., 2016). It has been found that forest growth and aboveground carbon storage are strongly determined by variations in mean tree size, stand basal area, and tree density (e.g., Gómez-Aparicio et al., 2011; Ruiz-Benito et al., 2014; Vayreda et al., 2012). Further, variations in tree size and stand density underlay competition from neighbors, which in turn influence growth (Condés et al., 2017; Gómez-Aparicio et al., 2011; Lechuga et al., 2017) and modulate drought-induced mortality events (Jump et al., 2017). In this respect, drought can also impact forest growth and mortality rates by delineating demography and species distribution ranges (e.g., Benito-Garzón et al., 2013; Changenet et al., 2021; Vilà-Cabrera et al., 2011) and by controlling the carrying capacity of the stands (Bravo-Oviedo et al., 2018). However, forest inventories do not always provide long-term annual measures of individual tree growth, hindering the assessment of drought impacts on tree growth (e.g., Sánchez-Salguero et al., 2013; Serra-Maluquer et al., 2018). Therefore, the combination of tree-ring databases with forest inventory data allow distance-dependent comparisons (Dye et al., 2016), and provide complementary and valuable information of forest dynamics in response to drought (Biondi, 1999; Etzold et al., 2019; Evans et al., 2017; Klesse et al., 2016; Ruiz-Benito et al., 2020; Sánchez-Salguero et al., 2013).

To quantify responses to drought from different data sources, we take advantage of an extensive network of cross-dated tree-ring data (hereafter abbreviated as RWI-net; see Gazol et al., 2020) with increment cores from 16 tree species (Appendix S1: Table S1) sampled across the Spanish Iberian Peninsula, and of the Spanish National Forest Inventory (hereafter abbreviated as NFI) sampling tree and plot level data each 1 km in forested areas. We aim to understand how the cumulative impact of droughts during the period 1981–2005 affected Spanish forests. We hypothesize that tree-ring vulnerability underlies forest responses to drought (i.e., growth, ingrowth, and mortality). We expect the cumulative impacts of drought to be stronger in drought-prone regions and particularly in gymnosperm forests affecting radial growth as well as the growth, ingrowth, and mortality of NFI plots. In particular, we expect that (1) RWI-net growth responses to severe droughts will display a stronger sensitivity in drought-prone regions, thus the cumulative impact of severe droughts will be stronger in arid than in milder sites, resulting in an spatially aggregated pattern of radial growth as well as in forest growth, ingrowth, and mortality; (2) NFI growth changes will be strongly dependent on initial structure, particularly stand density and basal area, but concurrently NFI plots will display lower growth and

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potentially greater mortality in sites more severely impacted by drought, thus resulting in a spatial covariation between RWI-net and NFI growth responses; and (3) RWI-net sensitivity to drought informs about forest vulnerability to drought, particularly in gymnosperms.

MATERIAL AND METHODS

Study area

The study covers the Spanish Iberian Peninsula and Balearic Islands (492,175 km^2; Figure 1), which represents a transitional area between temperate and Mediterranean climates. In general, humidity decreases from the north to south and from the west to east due to the contrasting influences of the Atlantic Ocean and the Mediterranean Sea, which also affect seasonal precipitation regimes (Martín-Vide & Olcina, 2001). Total annual precipitation in northern regions can reach up to 2000 mm, with maxima in winter and spring, whereas in the southeastern regions, the total annual precipitation ranges between 250 and 300 mm, often with maxima in autumn. Air temperature decreases towards the northern regions and with elevation. Several Eurosiberian tree species find their southern distribution limit (rear edge) in mountain areas of the Spanish Iberian Peninsula (e.g., *Abies alba* Mill., *Fagus sylvatica* L., *Pinus sylvestris* L., *Pinus uncinata* Ram., *Quercus robur* L., *Q. petraea* [Matt.] Liebl.). Natural regenerated forests coexist with pine plantations, which represent around 20% of the total forest area in Spain (FAO, 2013).

Spanish National Forest Inventory (NFI)

To quantify changes in forest growth, ingrowth, and mortality we used data from the second (NFI2; carried out in 1986–1996) and the third (NFI3; carried out in 1997–2007) Spanish National Forest Inventories (NFI), both established in the 1980s and continuously monitoring ever since the Spanish forests. The NFI consist of georeferenced, permanently established, circular plots of 25-m radius systematically distributed on a 1-km^2 cell grid over forested areas (cf. Villaescusa & Díaz, 1998). Inside each plot, each tree with a dbh > 75 mm and height >1.3 m was mapped. The 25-m radius plots are divided into subplots of 5-, 10-, 15-, and 25-m radii within which all trees with diameters at breast height (dbh) of 7.5–12.4, 12.5–22.4, 22.5–42.5, and ≥42.5 cm were measured, respectively. Each individual tree was also classified as dead or alive. Repeated measures over the same individuals are taken periodically (i.e., every ∼10 years), which allows quantifying demographic changes such as

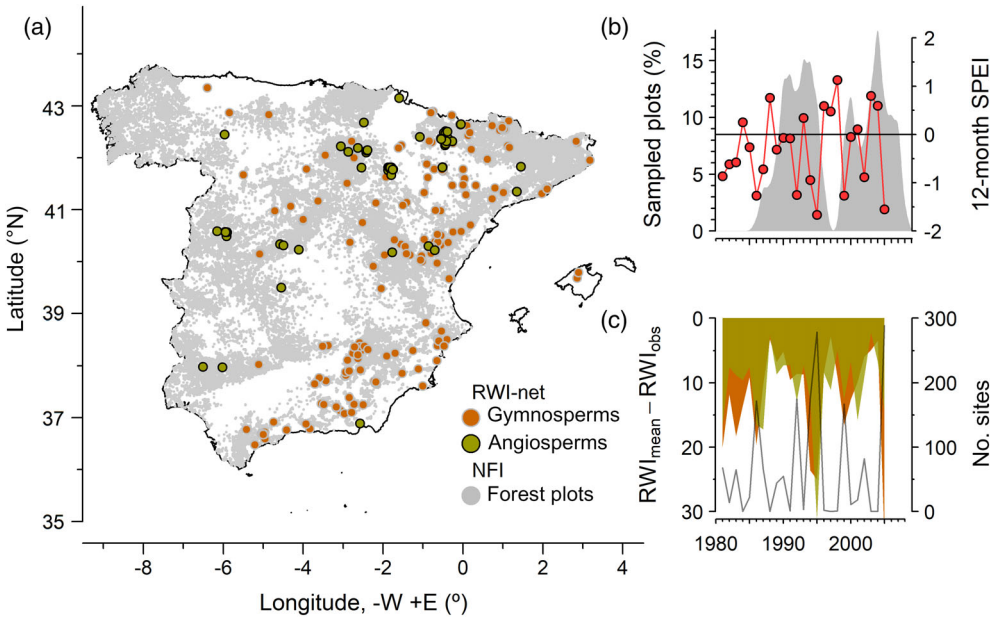

FIGURE 1 Relationships between the selected tree-ring sites (RWI-net) and the Spanish National Forest Inventory database (NFI). (a) Permanent NFI forest plots (gray areas) measured in Spanish forests with tree-ring width (RWI-net) sites overlapped: brown dots, gymnosperms; green dots, angiosperms. (b) Density of sampled NFI plots per year (in gray) and the 12-month-long June Standardized Precipitation–Evapotranspiration Index (SPEI) for the 1981–2005 period that informs about drought occurrence (continuous red line mean). (c) Growth reductions (RWI$_{mean}$ – RWI$_{obs}$, percentage) during the period 1981–2005 in the selected RWI-net populations separating angiosperms (green area) and gymnosperms (brown area). The black line (secondary *y*-axis) shows the number of sites for which the year was classified as drought (20% lowest SPEI values). Note that tree growth reductions were more common in dry years

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forest growth, ingrowth, and mortality between the NFI2 and the NFI3. In this study, we excluded NFI plots that were completely logged or have been burned by wildfires between consecutive inventories. Plots that were sampled in the third (NFI3) but not in the second (NFI2) inventory were also excluded. Forest growth was quantified as the increment in basal area (ΔBA, in m^2 ha^{-1} $year^{-1}$) of living trees between the two consecutive inventories (i.e., NFI2 and NFI3) divided by the number of years between inventories (Appendix S1: Figure S1a). Forest ingrowth (R; in m^2 ha^{-1} $year^{-1}$) was quantified as the basal area of trees sampled in NFI3 but not in NFI2 divided by the number of years between inventories. Forest mortality (in m^2 ha^{-1} $year^{-1}$) was quantified as the sum of the basal area (−ΔBA) of the trees sampled as alive in NFI2 and dead in NFI3 divided by the number of years between inventories. All basal area calculations were done at the individual tree level (m^2/ha) to account for the variable sampling radius plot (i.e., each NFI plot has four concentric subplots and the minimum tree size is different in each concentric subplot). The basal area at the plot level was calculated summing the basal area of each tree relative to hectare and, therefore, considering the concentric circle in which each tree was measured. With this method, we avoided biases in basal area calculations plots dominated by large of small tress, as it has been proved as an efficient and unbiased method for volume and basal estimation (Henttonen & Kangas, 2015).

Drought data

The Standardized Precipitation-Evapotranspiration Index (SPEI; Beguería et al., 2014; Vicente-Serrano et al., 2010) was used to assess drought severity. We calculated 12-month long June SPEI values for the period 1981–2005 in each plot, since this SPEI scale has been shown to be tightly related to tree growth in Spanish tree species (Pasho et al., 2011). To calculate SPEI, we used 1.1-km^2 gridded climatic data assembled at a weekly timescale (Vicente-Serrano et al., 2017). This high-resolution gridded data set was based on values of daily mean temperature, sunshine duration, wind speed, relative humidity, and precipitation, all available from the Spanish Meteorological Agency (AEMET). All available data sets were homogenized and quality checked prior to the estimation of gridded values (see Vicente-Serrano et al., 2017).

Bioclimatic variables were downloaded from the WorldClim data base (https://www.worldclim.org/data/bioclim.html) at a spatial resolution of 0.5″. We focused on four bioclimatic variables that influence cumulative drought impacts on forests: mean annual temperature and precipitation (bio1 and bio12, respectively), and temperature and precipitation seasonality (bio4 and bio15, respectively).

Tree-ring data (RWI-net)

We used an extensive network of cross-dated tree-ring chronologies (RWI-net, see Gazol et al., 2018; Vicente-Serrano et al., 2020) of annually resolved tree-ring width series from 29 tree species sampled across Spain to quantify tree growth and responses to climate. For this study, we selected 16 (9 gymnosperms and 7 angiosperms, Appendix S1: Table S1) out of these 29 tree species. All 16 species were sampled in at least two populations across their distribution ranges (Appendix S1: Table S1). We only included chronologies spanning at least the period 1981–2005.

Each of the populations included in this study was represented by 10 or 12 dominant or codominant trees (Gazol et al., 2018). Trees were cored at 1.3 m using Pressler increment borers to obtain from one to four wood cores per tree. These cores were air dried, mounted on wooden grooves, and sanded until tree-rings were clearly visible, which allowed the visual cross-dating of the samples (Fritts, 2001). The width of all tree-rings was measured to 0.01 mm resolution using a binocular microscope and measuring stands (Velmex, Lintab-TSAP). The COFECHA software was used to assess the accuracy of the visual cross-dating (Holmes, 1983).

To construct robust mean site chronologies, tree-ring width measurements were processed following dendrochronological protocols (Fritts, 2001). Individual tree-ring width measurements were detrended with a cubic smoothing spline with a 50% frequency response cutoff at 30 years. The observed tree-ring width measures were divided by the fitted values to obtain standardized ring-width indices. Finally, bi-weight robust means were used to average individual standardized ring-width series into mean site chronologies. Residual chronologies were obtained by prewhitening each series (i.e., removing autocorrelation) prior to averaging. These site, standard, and residual chronologies were scaled to have an exact mean of 1 for the period 1981–2005 in each population. These analyses were performed using the *dplR* library (Bunn et al., 2018).

Calculating drought impacts on tree growth and forest dynamics

To quantify the sensitivity of tree growth to drought, we selected the five most severe droughts that have affected each selected RWI-net population in the period 1981–2005 (Figure 1b and Appendix S1: Figure S2). The 12-month-long June SPEI values for the period 1981–2005 in each

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site were used for selecting droughts. Thus, drought years were selected for each site by considering the 5 years with the lowest SPEI values in that period.

Severe droughts were frequent across sites in 1986, 1994, 1995, 1999, and 2005 although other years such as 1992 were also considered dry in some populations (Figure 1b,c). In general, these droughts corresponded to growth reductions (Figure 1c and Appendix S1: Figure S2) and have triggered extensive forest dieback in many sites across the Spanish Iberian Peninsula (Camarero et al., 2015; Génova, 2012; Gazol et al., 2018, Sánchez-Salguero et al., 2018).

To test how the cumulative impacts of drought affected the growth of the sampled RWI-net populations, we calculated drought-induced cumulative growth reductions (CDI, cumulative drought impact) as the summed impact of the selected droughts on growth of each population (Appendix S1: Figure S1b). Drought impact was calculated as the difference between the mean growth during the period 1981–2005 and the observed growth during the drought year. Note that, since the mean growth equals 1, this is equivalent to a z score. Values >1 indicate that growth during drought was greater than average and so they were truncated to 0 (427 drought events: 26% of the situations). The cumulative impact of drought on growth was calculated as the summed values over the different droughts (Appendix S1: Figure S1b). We used standard chronologies to quantify drought impacts and their cumulative effect because standard chronologies account for potential autocorrelative effects when two droughts occur consecutively (or in a relatively short period of time). Further, preliminary analyses showed that similar results were obtained when using either standard or residual chronologies (Appendix S1: Figure S3).

To assess the relationship between plot level NFI-estimated growth, ingrowth and mortality, and the cumulative impact of drought on RWI-net growth estimations, we used a distance approach. For each NFI plot, we selected those RWI-net populations of the same species dominating the NFI plot (i.e., the species accounting for 60% of the basal area of the plot) that were located at a distance lower than 10 km (Appendix S1: Figure S1a). Thus, for each NFI plot, we considered the cumulative impact of drought of the RWI-net site located less than 10 km away to the NFI plot. Second, we quantified the number of severe droughts to which each NFI plot was exposed to by counting the number of droughts with stand growth reductions higher than 50% between NFI2 and NFI3. Severe droughts were defined as those having an SPEI lower than the selected threshold and growth reductions higher than 50% for the nearby RWI-net population (i.e., drought impact for the selected drought >0.5; for further details see Appendix S1: Figure S1). A total of 334 RWI-net sites with chronologies that covered the period 1981–2005 for the 16 species, were finally used. For 192 of these RWI-net sites, 1883 NFI plots were found at distances <10 km (Appendix S1: Table S1).

Statistical analyses

We used spatial autocorrelation techniques to describe the patterns of the cumulative drought impacts observed in the RWI-net population and the growth, ingrowth, and mortality of the selected NFI plots. For this purpose, we used spline correlograms, which is a generalization of spatial correlograms (Bjørnstad & Falck, 2001). For each variable, correlograms were calculated up to 200 km and the significance was estimated by generating a bootstrapped distribution (999 resamples). Finally, cross-correlograms were applied to estimate the spatial dependency between the cumulative drought impacts (RWI-net) and the observed growth, ingrowth, and mortality (NFI).

Autocovariate regression was used to study the effect of bioclimatic variation on cumulative drought impacts in the RWI-net populations (Dormann et al., 2007). This procedure relies on the inclusion of a spatial autocovariate as an additional explanatory variable into a linear model to account for spatial autocorrelation. Thus, we studied the effect of different bioclimatic variables while accounting for spatial autocorrelation in cumulative drought impacts. We fitted the full models using ordinary least square regression and evaluated them through the increase in the Akaike Information Criterion (ΔAIC) with respect to the model showing the lowest AIC, using model comparison and averaging to select the model and to assess the relative importance (Akaike relative weight) of each variable (Burnham & Anderson, 2002).

To evaluate whether the occurrence of abrupt growth reductions in the corresponding RWI-net population correlates with forest growth reductions or enhanced forest mortality in NFI plots, we compared the forest growth (ΔBA), ingrowth (R), and mortality ($-\Delta$BA) between plots that were exposed to different numbers of severe droughts. The Dunnett's modified Tukey-Kramer pairwise multiple comparison test (Dunnett, 1980) was used to compare NFI plots in the neighborhood of the RWI-net populations displaying growth reductions in response to none, one or two droughts. Furthermore, we also compared if the occurrence of two severe droughts showed different impact depending on whether such droughts occurred in consecutive or separated years.

Autocovariate spatial regressions were also used to evaluate how cumulative drought impacts was related to changes in forest growth (ΔBA), ingrowth (R), and forest mortality ($-\Delta$BA). We created models including RWI-net based cumulative drought impacts and other covariates

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that may influence changes in forest growth and structure and can be related with tree to tree competition. We tested the influence of the bioclimatic variables listed above, the mean dbh (mDBH, mm) of the trees from the second inventory (NFI2), as well as the basal area of the plot (BA, m^2/ha) and the tree density (Dens, trees/ha) recorded in the second inventory (NFI2) and the minimum 12-month-long SPEI to account for a metric of drought independent on growth. ΔBA, R and −ΔBA were log-transformed ($\log[x+1]$) prior to the analyses. Furthermore, standardized coefficients were calculated for the explanatory variables to facilitate the interpretation of their effect (Schielzeth, 2010).

Separate models were created for gymnosperms and angiosperms. In the case of mortality, NFI plots in which mortality was zero were not included in the autocovariate regression analysis (around 60% were removed). However, these plots were considered for the spatial correlation and cross-correlation, and the Dunnett analyses.

All statistical analyses were performed in R 3.5.2 (R Core Team, 2018). The *dplR* package (Bunn et al., 2018) was used to calculate ring-width index (RWI) and mean site chronologies, the *raster* package to manage spatial data (Hijmans, 2019), the *ncf* package (Bjørnstad, 2020) was used to calculate spline-correlograms, the *spdep* package (Bivand et al., 2013) was used for the autorregresive modeling. Finally, the *MuMIn* (Barton, 2012) package was used to perform the multi-model selection.

RESULTS

Cumulative drought impacts on growth prevail in dry regions, particularly for gymnosperms

We found a significant positive autocorrelation in the cumulative drought impacts on tree growth for gymnosperms (Figure 2). For angiosperms, the spatial autocorrelation was not significant (Figure 2), suggesting that the positive significant autocorrelation found when all sites are analyzed together is caused by the higher weight of gymnosperm forests. Along this, the cumulative impact of drought on tree growth was higher for gymnosperms than for angiosperms (Appendix S1: Figure S4). The total annual precipitation was the main factor driving the biogeographical variation of cumulative drought impacts both for angiosperms and gymnosperms (Figure 2b and Table 1). Cumulative drought impacts were more pervasive in dry regions, particularly in forests dominated by gymnosperms (mostly pine species) from the semiarid southeastern Spain (Figure 2b).

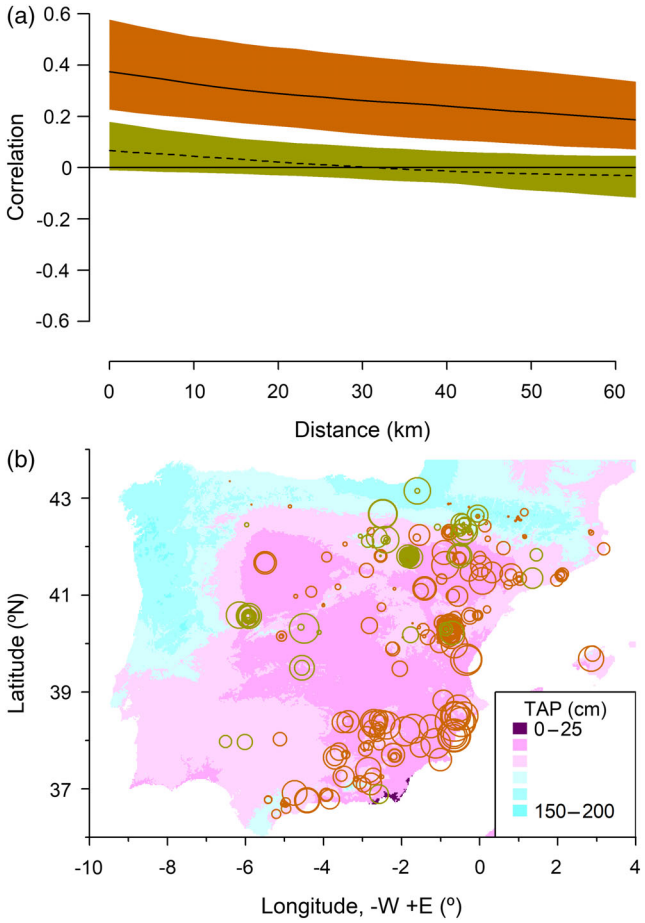

FIGURE 2 Spatial autocorrelation and biogeographical patterns of cumulative drought impacts on tree growth. (a) The spatial autocorrelation of cumulative drought impact in angiosperms (dashed line and green area represent the mean correlation and 95% confidence intervals, respectively) and gymnosperms (solid line and brown area represent the mean correlation and 95% confidence intervals, respectively). (b) The biogeographical distribution of cumulative drought impacts on tree growth (size of the dots) in angiosperm- (green symbols) and gymnosperm-dominated (brown symbols) forests. The background color represents the total annual precipitation (TAP)

Drought decreased stand growth and increased mortality, especially for gymnosperms

We found a negative spatial cross-correlation between cumulative drought impacts on tree growth and stand growth (see magnitude of negative values in Appendix S1: Figure S5). In other words, large radial-tree growth reductions in response to droughts in RWI-net populations converged with reduced stand growth in nearby NFI forests at distances up to 50 km (angiosperms) or 150 km (gymnosperms). This pattern was particularly evident in gymnosperm forests (Appendix S1: Figure S5). Similar results

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TABLE 1 Autocovariate regression models relating cumulative drought impacts on the growth of forest dominated by gymnosperms and angiosperms with the bioclimatic variables. For each variable, the coefficient (±SE) according to a conditional model averaging and the variable relative importance are shown

	Gymnosperms		Angiosperms	
Variables	**Coefficient ± SE**	**Importance**	**Coefficient ± SE**	**Importance**
Annual mean precipitation	−0.34 ± 0.14*	0.99	−0.37 ± 0.15*	0.93
Annual mean temperature	0.39 ± 0.13**	0.92	0.09 ± 0.19	0.30
Precipitation seasonality	0.12 ± 0.09	0.48	−0.18 ± 0.16	0.42
Temperature seasonality	−0.10 ± 0.07	0.51	−0.12 ± 0.21	0.36

*$p < 0.05$; **$p < 0.01$.

were obtained when cumulative drought impacts on growth were cross-correlated with forest ingrowth, but no significant spatial cross-correlation was found between cumulative drought impacts on growth and nearby forest mortality either in angiosperms or gymnosperms (Appendix S1: Figure S5). In agreement with this, the spatial correlation of forest growth and ingrowth was significant at distances up to 20–30 km, whereas the pattern in mortality showed less spatial autocorrelation and up to distances of 10–20 km (Appendix S1: Figure S6).

Drought-induced severe growth reductions (i.e., higher than 50%) were more common in gymnosperms than angiosperms (~33% vs. 15% of the studied sites, respectively). For angiosperms, two drought-induced severe growth reductions between NFI2 and NFI3 were not observed, whereas for gymnosperms they were observed in 17% of the sites studied (i.e., 297 forests). For angiosperms, forest growth and ingrowth were significantly greater near RWI-net populations not impacted by drought (Figure 3a,b), while higher mortality rates in stands not impacted by drought were observed (Figure 3c). For gymnosperms, the occurrence of one or two severe droughts caused strong reductions in forest growth and ingrowth (Figure 3a,b), which were even stronger when the two droughts occurred consecutively (Table 2). A significant increase in mortality of gymnosperms was observed in forests impacted by two droughts (Figure 3c) with no differences between the droughts occurring separated or consecutively.

Tree growth sensitivity to drought as a critical driver of forest dynamics, particularly for gymnosperms

Forest growth was significantly influenced by tree growth sensitivity to drought when covariates were not included in the model (Appendix S1: Figure S7). In the case of mortality, this effect was significant for gymnosperms only. As expected, the effect of drought sensitivity was not the most important driver of forest changes in stand basal area when the climatic and structural covariates were included in the models (Figure 4 and Appendix S1: Table S2). Forest growth and ingrowth increased with initial stand density and basal area (Figure 5a,b), whereas these variables had disparate impacts on mortality (Figure 5c). In general, forest growth decreased, and forest mortality increased with tree sensitivity to drought (i.e., accumulated growth decreases in response to drought; Figure 4 and Appendix S1: Table S2). The relationships between tree growth and forest changes in stand basal area were more important (i.e., significant in the case of growth and mortality) for gymnosperms than for angiosperms (Figure 4, Appendix S1: Table S2 and Figure S7).

DISCUSSION

We found a spatial imprint in the cumulative impact of drought on tree growth and changes in forest stand basal area during the transition from the 20th to the 21st century in Spain. Severe droughts particularly impacted the gymnosperms from dry sites, highlighting the great sensitivity to drought of these species. Our results were obtained by using two independent data sets: an extensive tree-ring network (RWI-net) and permanent plot (NFI) data resurveys covering the range from Atlantic to Mediterranean climates of the Spanish Iberian Peninsula. According to our main hypothesis, we found common signals of drought-induced tree growth on stand forest dynamics particularly for gymnosperms and dry regions. We also found greater forest growth reductions and mortality increases in the case of gymnosperms when tree growth reductions were strongly impacted by drought, as stated by our second hypothesis. Notably, these drought impacts were more evident in gymnosperms than in angiosperms probably due to the more frequent distribution of gymnosperms in drought-prone regions, but also because of their higher representativeness in our data

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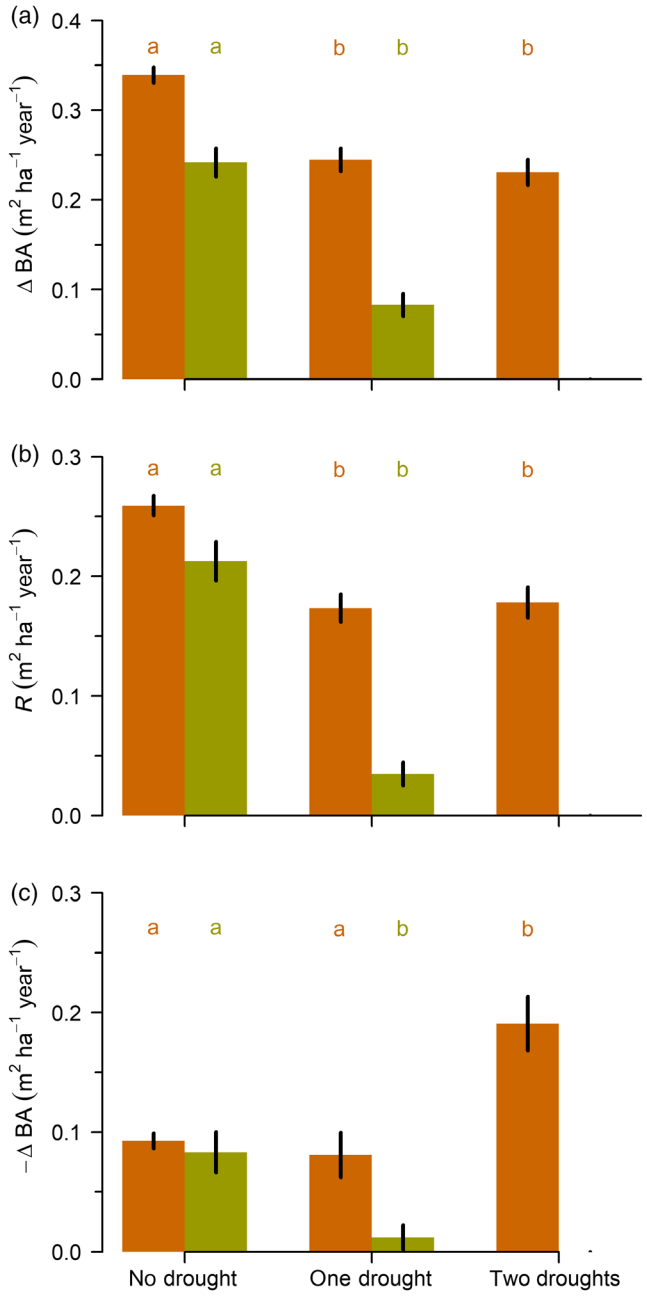

FIGURE 3 Forest demographic rates including (a) growth increment in stand basal area (ΔBA), (b) ingrowth or increment in stand basal area due to recruited individuals (R), and (c) mortality or basal area loss ($-\Delta$BA), measured in NFI plots as a function of drought frequency and severity. Different colors are used for angiosperms (green bars) and gymnosperms (brown bars) across drought frequency classes: no drought and one and two droughts. The bars represent the mean values and the lines the standard error for the mean. The letters above the bars represent the existence of significant differences ($p < 0.05$) in growth, ingrowth, or mortality between sites experiencing different drought frequencies

set. Nonetheless, our third hypothesis was partially supported, stating that tree growth reductions determine forest growth and mortality patterns because initial stand conditions were the main factors determining changes in growth. Hence, we obtained a weak effect of tree sensitivity to drought on changes in stand basal area when the structural covariates were accounted for (see Figure 4). Our study indicates that combining different sources of information (i.e., plot resurveys, NFI; and tree-ring widths, RWI-net), despite challenging, may provide valuable and complementary information on forests responses to drought across multiple spatial and temporal scales (see also Babst et al., 2018; Gazol et al., 2018; Kannenberg et al., 2019; Khoury & Coomes, 2020; Ruiz-Benito et al., 2020; Sánchez-Salguero et al., 2013; Zhang et al., 2017). However, our results also evidence that site differences make difficult to obtain solid conclusions and, therefore, a complete picture on forest responses to climate change can be obtained from the Spanish National Forest Inventory and the quantification of "in situ" tree-ring widths samplings. This will also allow to determine how initial stand conditions such as density interacts with tree sensitivity to drought on modulating forest growth.

Convergence between tree growth sensitivity to drought and changes in forest stand basal area patterns

We found a positive tree–forest growth cross-correlation that could be related to a common climatic signal, which determines secondary growth both in tree ring (RWI-net) and forest inventory data sets (NFI). The cumulative impact of drought on tree and forest stand basal area growth were positively cross-correlated (Appendix S1: Figure S5). However, the moderate magnitude of the correlation coefficients suggests a strong impact of local factors that can modulate tree sensitivity to climate and growth production (Monserud & Sterba, 1996; Sánchez-Salguero et al., 2015) such as stand structure (Gómez-Aparicio et al., 2011), soil water holding capacity and nutrient availability (e.g., Manrique-Alba et al., 2017; Marchand et al., 2019). The moderate impact of drought-induced tree responses on forest dynamics was even clearer in the case of mortality, probably because local factors play a key role (e.g., tree-to-tree competition and soil moisture availability; Hartmann et al., 2018). This is particularly evident in the case of angiosperms, where we found lower mortality in forests impacted by drought. Given that many Iberian angiosperm forests are still in an early successional stage, self-thinning because of competition for space and light might be more important than drought for driving mortality patterns (cf. Astigarraga et al., 2020). However, we found no significant impacts of stand density on forest mortality in

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TABLE 2 Differences in gymnosperm's stand growth, ingrowth, and mortality between Spanish National Forest Inventory (NFI) plots situated near RWI-net (network of cross-dated tree-ring data) sites that were affected either by two separate or two consecutive droughts

	Two separate droughts	Two consecutive droughts	Dunnett test
Growth	0.266 ± 0.017	0.133 ± 0.020	−0.133 (−0.185 to −0.081)
Ingrowth	0.203 ± 0.016	0.108 ± 0.018	−0.094 (−0.142 to −0.047)
Mortality	0.184 ± 0.026	0.210 ± 0.047	0.026 (−0.080 to 0.132)

Note: Note that angiosperms forests could not be tested because sites suffering two droughts between NFI2 and NFI3 were absent. The mean values of forest growth, ingrowth, and mortality together with the SE are shown. Significant differences ($p < 0.05$) are based on the Dunnett's modified Tukey-Kramer pairwise multiple comparison test (the confidence interval for the test statistic does not include 0).

the case of angiosperms, suggesting that our capacity to explain changes in angiosperms mortality is more reduced.

We found greater drought-induced growth sensitivity in gymnosperms than angiosperms, which also resulted in a stronger spatial autocorrelation of drought impacts (Figure 2). Our results agree with recent temporal trends in the Iberian forests suggesting increased mortality and reduced growth in gymnosperms when compared to angiosperms (Astigarraga et al., 2020), and it could be related to contrasting drought-avoidant and drought-resistant strategies that confers them contrasting vulnerability to drought (Greenwood et al., 2017; Khoury & Coomes, 2020; Ruiz-Benito, Ratcliffe, Zavala, et al., 2017). Furthermore, the increased sensitivity of forests dominated by gymnosperms could be strongly influenced by marked differences in their distributional patterns across Spain (Figure 1). On the one hand, conifer forests studied cover the entire climatic range in the Spanish Iberian Peninsula (Costa et al., 2005), but a high proportion of gymnosperm-dominated forests are in the most arid regions of the Iberian Peninsula (Ruiz-Benito et al., 2012). On the other hand, angiosperms are more abundant in regions with mild, wet climatic conditions (see Figure 1). Overall, the distribution of species along the water availability gradients of the Iberian Peninsula markedly influences both stand characteristics and forest productivity (Alberdi et al., 2010; Benito-Garzón et al., 2013; Gómez-Aparicio et al., 2011; Vayreda et al., 2012). For example, this is reflected in the amplitude of the gradients in stand density covered in our study, which is longer in the case of angiosperms (Figure 5).

Gradients in water availability may determine changes in angiosperm and gymnosperm productivity (Khoury & Coomes, 2020; Vayreda et al., 2012) due to their impacts on stand density (Condés et al., 2017). However, the covariation between cumulative drought impact on tree and stand growth and ingrowth suggests that stand-level changes in stand basal area are partially modulated by drought-induced tree-level responses. Our results are in line with the greater sensitivity to drought of gymnosperms, also in terms of lasting drought legacies (Anderegg et al., 2015; Greenwood et al., 2017), which is also supported by their greater drought vulnerability (Appendix S1: Figure S4). However, the spatial gradient in water availability can induce strong changes in growth responses to climate (Lebourgeois et al., 2012) and drought (Gazol, Camarero, et al., 2017; Gazol, Ribas, et al., 2017; Sánchez-Salguero et al., 2015, 2018). The relatively frequent presence of drought-tolerant gymnosperms in the driest south-eastern Spanish Iberian regions (where droughts are more common and intense as e.g., *Pinus halepensis*) and the prevalence of productive angiosperms in the wettest regions (less impacted by drought; Gazol et al., 2018 and see Figures 1 and 2) might be determining the greater drought vulnerability in gymnosperms than angiosperms.

Drought-induced tree-level effects on stand growth, ingrowth, and mortality depend on drought frequency and functional groups

The frequency of severe droughts caused abrupt tree growth reductions (Figure 1b,c) and, accordingly, nearby forests had lower growth rates than forests where no drought occurred (Figure 3). Interestingly, drought-induced effects on forest growth and mortality were in general significant, pointing to the convergence between RWI-net and NFI responses to drought. The impact of tree responses on changes in forest stand basal area might be due to the spatial characteristics of droughts, which can impact across broad regions (Vicente-Serrano et al., 2017). At smaller scales, local factors influencing tree growth might play a more relevant role masking the regional drought signal (Caminero et al., 2018; Tardif et al., 2003). Thus, part of the relationship between tree and forest growth might be due to local variations in key drivers of tree responses to drought such as microsite, topography or soil conditions that can differ across species (Camarero et al., 2017; Gazol, Camarero, et al. 2017; Gazol, Ribas, et al., 2017; Gazol et al., 2018; Sánchez-Salguero et al., 2015, 2018), and between

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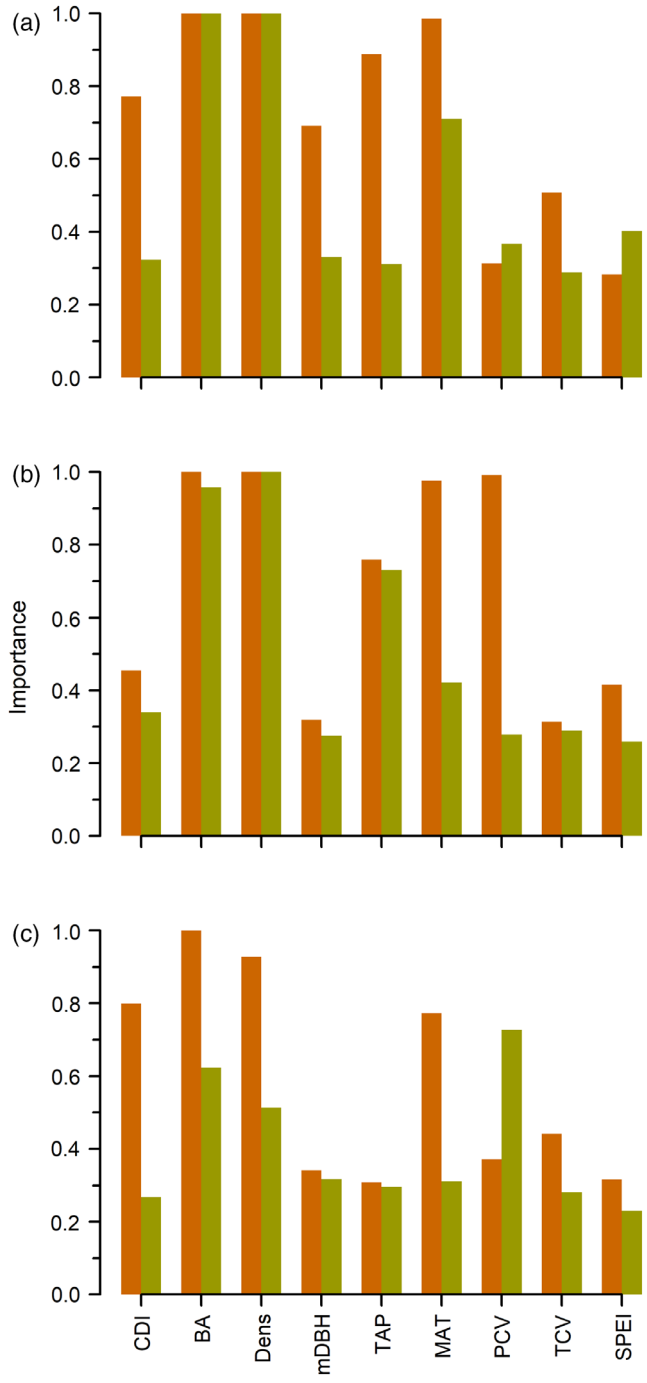

FIGURE 4 Importance of cumulative drought impact on growth in autocovariate models of (a) forest growth (rate of increase in basal area, ΔBA), (b) forest ingrowth (new individuals, *R*), and (c) forest mortality (rate of decrease in basal area, −ΔBA) in angiosperms (green bars) and gymnosperms (brown bars). Bar length is proportional to the Akaike relative weight (importance) of each variable in the models, the larger the value the greater the importance. Variables are CDI, cumulative drought impact; BA, stand basal area in NFI2; Dens, stand density in NFI2; mDBH, stand mean diameter at breast height in NFI2; TAP, total annual precipitation; MAT, mean annual temperature; PCV, precipitation variability (coefficient of variation); TCV, temperature variability (coefficient of variation); SPEI, the minimum 12-month-long SPEI between NFI2 and NFI3

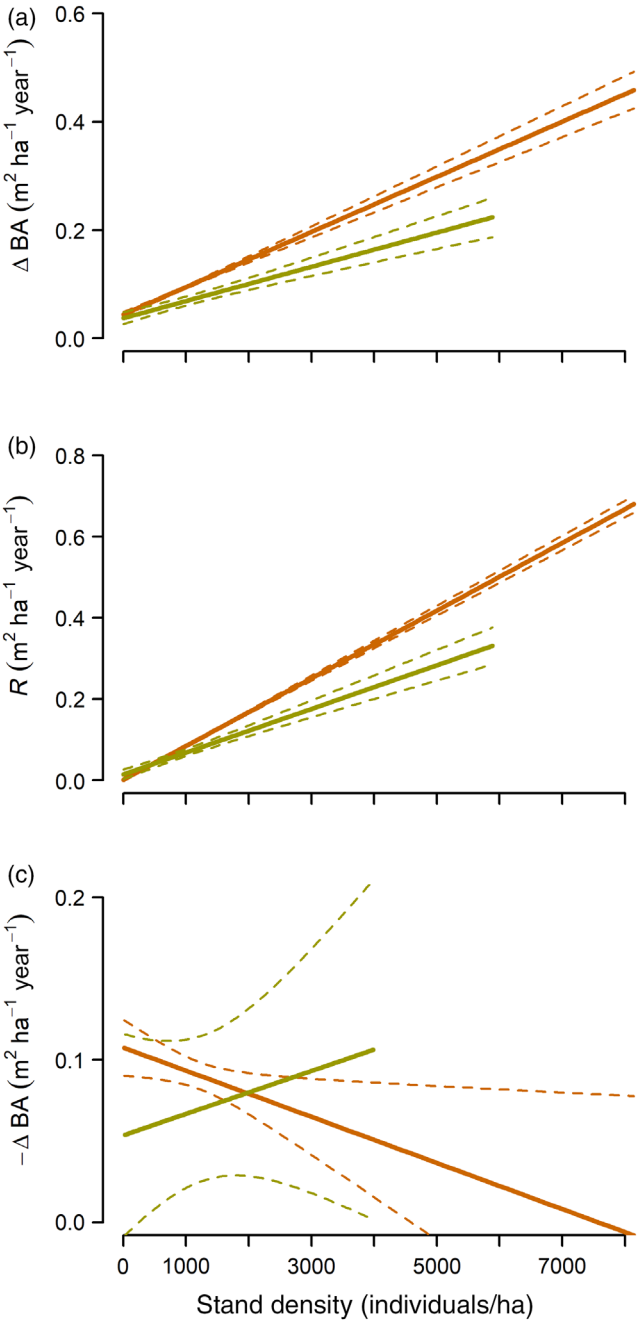

FIGURE 5 Relationships observed between initial stand density (stand density in NFI2) and forest demographic rates, including (a) growth increment in stand basal area (ΔBA), (b) ingrowth or increment in stand basal area due to recruited individuals (*R*), and (c) mortality or basal area loss (−ΔBA), measured in NFI plots as a function of drought frequency and severity. The continuous and dashed lines show the fitted regression and its 95% confidence intervals for gymnosperms (brown lines) and angiosperms (green lines)

populations within the same species (Linares & Tíscar, 2011, Gazol, Camarero, et al., 2017, Sánchez-Salguero et al., 2018, Sangüesa-Barreda et al., 2019, Serra-Maluquer et al., 2019).

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We did not find evidence for greater growth reductions with the increase in drought frequency (i.e., from one to two droughts, Figure 3). However, when such droughts occurred consecutively the growth of nearby forests was more impacted in line with previous studies (Anderegg et al., 2020). This suggests that drought legacies can be easier to detect in forests dominated by gymnosperms, where ecological memory plays a relevant role (e.g., Anderegg et al., 2015; Peltier et al., 2016). Previous results reported abrupt growth reductions in mortality responses to droughts lasting more than 1 year as being common in gymnosperms (Cailleret et al., 2017). Notably, the occurrence of two droughts, either separately or consecutively, resulted in a marked increase in gymnosperm mortality (Figure 3). However, two severe droughts were not detected in sites dominated by angiosperms, which might lead to underrepresented sampling. This might be because most angiosperm populations come from less drought-prone regions and angiosperms are less represented in our study sites as the number of tree-ring width series was half the number of gymnosperm series (see also Gazol et al., 2018). Caution is thus required when interpreting the results of multiple droughts.

Scaling up tree sensitivity to drought to stand dynamics

After illustrating the existence of a positive link between tree and stand growth by studying tree-ring and inventory data sets, we could expect a significant influence of drought sensitivity, as a surrogate of forest vulnerability to drought, on forest basal area changes, which might be partially attributable to the direct impact of drought but also to the existence of drought legacy effects (Anderegg et al., 2015). We found lower growth and ingrowth, and higher mortality rates in forests located near more RWI-net populations accumulating larger drought impacts, this association being more marked in gymnosperms. Stronger and more pervasive legacy effects of drought on growth can be expected in major families of gymnosperms (e.g., Pinaceae) than in angiosperms (e.g., Fagaceae) according to Anderegg et al. (2015). Such legacies also influence their post-drought resilience and mortality rates (DeSoto et al., 2020). We did not test for the impact of legacies of drought on growth, because their occurrence is strongly variable between sites and species (Gazol et al., 2020) and it would require the data to be gathered in the same stands. The only exception to this is when two droughts occur consecutively, or almost, and so the impact of the first year can affect growth reductions in the next year. In such cases, we have seen that growth reductions in nearby stands are more marked that when droughts occur separately (Figure 3), pointing again to the possible impact of legacies. Thus, the convergent patterns found between our two independent data sets suggest that drought and related legacy effects can affect stand dynamics. Drought reduces photosynthetic activity and increases the risk of xylem embolism thus reducing hydraulic conductivity, growth, and increasing the risk of tree death (Brodribb et al., 2010; Cailleret et al., 2019). Higher wood density and the ability to enable partial dieback to avoid drought might make angiosperms (e.g., Fagaceae species) less susceptible to drought than coexisting Pinaceae species (Greenwood et al., 2017). A trend towards greater dominance of angiosperms over gymnosperms has been observed in temperate forests (Alfaro-Reyna et al., 2018), which might be partially explained by trait variations between these two functional groups driving their post-drought successional dynamics (Ruiz-Benito, Ratcliffe, Zavala, et al., 2017). However, longer time studies are required to evaluate how forest composition will evolve in the future in response to hotter droughts and consider the potential influence of other land use legacies and demographic processes such as recruitment (Lines et al., 2020).

We found an effect of drought vulnerability on forest growth and mortality, even when structural and climatic variables were included as covariates in the models. However, caution is required due to the existence of multiple sources of variation in the forest growth rates estimated from NFI plots with climate accounting for a relatively lower percentage of explained variability than structural factors (e.g., Ruiz-Benito et al., 2014). We found that stand density has a strong positive impact on forest growth and ingrowth suggesting the importance of carrying capacity on determining growth along regional climate gradients. How initial stand density modulates forest growth can vary along climate gradients and depending on species-specific traits (Bravo-Oviedo et al., 2018; Condés et al., 2017), thus partially accounting for the impacts of drought vulnerability. Furthermore, forests responses to drought were quantified relying solely on basal area changes without accounting for changes in forest productivity, primary growth (leaf, shoot, and root production; e.g., Khoury & Coomes, 2020), fruiting or regeneration (e.g., Camarero et al., 2018; Kannenberg et al., 2019). Secondly, tree-ring data comes from living, dominant or codominant individuals, which are preferentially sampled in extreme populations to strengthen the climatic signal (Fritts, 2001), and the response of either dead (often fast-growing individuals) or suppressed individuals is often missing (Alexander et al., 2018; Babst et al., 2018; Brienen et al., 2017; Klesse et al., 2018). This contrast with the data coming from plot resurveys where all the individuals surpassing a size threshold are measured. Consequently, we based our estimations of drought impacts on growth in dominant, and mostly healthy, trees and compared it with the dynamic of dominant and

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suppressed trees in a stand. However, the fact that we found a signal of tree vulnerability on forest level responses is relevant because tree vulnerability had generally a lower effect compared to other local factors and, therefore, further studies considering more refined data sets, for example, evaluating tree and growth relationships with data derived from complete samplings of tree populations along altitudinal gradients (e.g., Sánchez-Salguero et al., 2015), are required to further understand the scalability from individual trees to forest stands. The dendrochronological sampling of trees in NFI plots along environmental gradients may provide complementary information on forest dynamics and tree growth and allow testing if tree-ring records are related to other stand characteristics such as changes in density or regeneration. For example, the positive effect of initial stand density on forest growth and ingrowth turned negative for mortality in the case of gymnosperms (Figure 5). It has been found that the impact of density on growth varies along humidity gradients (Condés et al., 2017) as does the role of drought tolerance on determining maximum density (Bravo-Oviedo et al., 2018). Thus, we can expect a covariation between tree response to drought and stand density on determining changes in stand growth, which might also vary from angiosperm to gymnosperm dominated forests (see, e.g., Jump et al., 2017; Zhang et al., 2017). In this respect, we found that the relationship between initial stand density and forest growth and ingrowth was stronger in the case of gymnosperms than for angiosperms. How stand density modulates growth and mortality depends on climate, but it also varies depending on stand age and across species (Condés et al., 2017) making difficult to drive strong conclusions with the studied data. Thus, testing such hypothesis will require a more refined within site determination of both, density, and tree growth response to drought, and this aim is outside the scope of this study.

Conclusions

We compared tree growth assessments based on individual tree-ring width data (RWI-net) with forest dynamics based on inventory plot structural (NFI) data demonstrating the existence of a common regional climate signal suggesting scalability of responses from trees to forests. The coherent signal in the two data sets allowed us to detect how tree vulnerability to drought can determine regional stand and forest structural responses depending on the forest type. We showed that high mortality rates at regional scales can be expected in forests dominated by gymnosperms and severely impacted by drought (i.e., those located in dry regions), in terms of tree growth reduction and increased vulnerability. Overall, our results show that changes in tree ring-width index in response to drought (i.e., sensitivity measures) may be used as an early warning signal to pinpoint forests particularly vulnerable to drought at regional scales (i.e., those stands showing low growth and high mortality rates).

ACKNOWLEDGMENTS

This study was financially supported by Xunta de Galicia, Grant/Award Number PGIDIT06PXIB502262PR, GRC GI-1809; INIA, Grant/Award Number RTA2006-00117; CANOPEE, 2014-2020-FEDER funds, Spanish Science Ministry RTI2018-096884-B-C31, RTI2018-096884-B-C33, AGL2017-83828-C2-2R, RTI2018-096884-B-C3,1 and RTI2018-096884-B-C32 projects. Gabriel Sangüesa-Barreda was supported by a "Juan de la Cierva-Formación" grant from MINECO (FJCI 2016-30121). Antonio Gazol and Paloma Ruiz-Benito were supported by a project "2018 Leonardo Grant for Researchers and Cultural Creators, BBVA Foundation." Ana-Maria Hereş was supported by the project PN-III-P1-1.1-TE-2019-1099 financed by the Romanian Ministry of Education and Research through UEFISCDI. Raúl Sánchez-Salguero was supported by VULBOS project (UPO-1263216, FEDER Funds, Andalusia Regional Government, Consejería de Economía, Conocimiento, Empresas y Universidad 2014-2020). Paloma Ruiz-Benito was supported by the Community of Madrid Region under the framework of the multi-year Agreement with the University of Alcalá (Stimulus to Excellence for Permanent University Professors, EPU-INV/2020/010) and the University of Alcalá "Ayudas para la realización de Proyectos para potenciar la Creación y Consolidación de Grupos de Investigación." Andrea Hevia was supported by PinCaR project (UHU-1266324, FEDER Funds, Andalusia Regional Government, Consejería de Economía, Conocimiento, Empresas y Universidad 2014-2020). The foundation accepts no responsibility for the opinions, statements and contents included in the project and/or the results thereof, which are entirely the responsibility of the authors.

CONFLICT OF INTEREST

Authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Gazol et al., 2022) are available in Dryad at https://doi.org/10.5061/dryad.sj3tx965x.

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SUPPORTING INFORMATION

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How to cite this article: Gazol, Antonio, J. Julio Camarero, Raúl Sánchez-Salguero, Miguel A. Zavala, Xavier Serra-Maluquer, Emilia Gutiérrez, Martín de Luis, et al. 2022. "Tree Growth Response to Drought Partially Explains Regional-Scale Growth and Mortality Patterns in Iberian Forests." *Ecological Applications* 32(5): e2589. https://doi.org/10.1002/eap.2589

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